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ANATOMY OF *SHINKAILEPAS MYOJINENSIS* SASAKI, OKUTANI & FUJIKURA, 2003 (GASTROPODA: NERITOPSINA)

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ABSTRACT

The anatomy of *Shinkailepas myojinensis* Sasaki, Okutani & Fujikura, 2003, was examined by gross dissection, scanning electron microscopy, and histological serial sections. The organization of the soft part conforms to general neritopsine pattern, especially in pallial complex, digestive system, reno-pericardial system, and nervous system. New character states previously unknown in neritopsine gastropods were revealed mainly in female and male reproductive systems, sense organs, and glands in pallial cavity. Comparison of our observations with published descriptions of various gastropods confirmed that the species of *Shinkailepas* are assigned to the superfamily Neritoidea among Neritopsina. The inclusion of *Shinkailepas* in the family Phenacolepadidae as in previous studies is also supported, although the number of their uniquely shared character is rather limited. Infrafamilial taxa of phenacolepadids so far anatomically studied are clearly divisible into deep-sea (*Shinkailepas* and *Olgasolaris*) and shallow-water (*Phenacolepas* and *Cinnalepeta*) groups in characters of the shell, operculum, head-foot external morphology, mantle margin, digestive tract, and female reproductive organ. At species level, members of *Shinkailepas* are diagnosed by morphology of the eye stalks, epipodial fold, and penis, as well as shell, radular and opercular characters.

Keywords: *Shinkailepas*, Phenacolepadidae, Neritopsina, comparative anatomy.

INTRODUCTION

In the recent systematics, Neritopsina includes six to nine families, namely, Neritidae, Neritiliidae, Phenacolepadidae, Hydrocenidae, Neritopsidae, including Titiscaniidae, and three helicinoidean families (Helicinidae, Ceresidae, and Proserpinidae, or three subfamilies of Helicinidae) (Thompson, 1980; Ponder, 1998; Sasaki, 1998; Kano & Kase, 2000, 2002). They comprise a robust clade phylogenetically (Ponder & Lindberg, 1997; Sasaki, 1998) and exhibit remarkable ecological diversification from deep-sea to terrestrial habitats (Kano et al., 2002; Sasaki & Ishikawa, 2002). Among them, three genera, *Shinkailepas*, *Olgasolaris*, and *Bathynerita,* have been known only from deep-sea chemosynthesis-based biological communities. The first two genera are currently assigned to the Phenacolepadidae (Beck, 1992; Warén & Bouchet, 2001; Sasaki et al., 2003), together with the shallow-water genera *Phenacolepas* and *Cinnalepeta*, and *Bathynerita* is regarded as a member of the Neritidae (Warén & Bouchet, 1993, 2001). They represent part of characteristic molluscan elements endemic to vent/seep environments.

In the genus *Shinkailepas* Okutani, Saito & Hashimoto, 1989, four species have been hitherto described: (1) *S. kaikatensis* Okutani, Saito & Hashimoto, 1989, from Kaikata Seamount, off Ogasawara Islands, Japan, 470 m deep, (2) *S. tufari* Beck, 1992, from Manus Back-Arc Basin, 2,450–2,505 m deep, (3) *S. briandi* Warén & Bouchet, 2001, from Mid-Atlantic Ridge, Menez Gowen to Logatchev site, 850–3,500 m deep, and (4) *S. myojinensis* Sasaki, Okutani & Fujikura, 2003, from Myojin Knoll, Ogasawara Ridge, Japan, 1,260–1,340 m deep. In addition, unidentified species were also reported from Mariana Back-Arc Basin (Hasegawa et al., 1997) and Okinawa Trough (Sasaki et al., 2003), suggesting the presence of more new species in the genus.

Although some anatomical descriptions have been published (e.g., Fretter, 1984; Sasaki, 1998; Kano & Kase, 2002), there is considerable uncertainty in anatomical organization of phenacolepadids and other possibly related

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neritoidean groups. Hence, further anatomical comparison is significant to understand relationships among *Shinkailepas*, *Olgasolaris*, shallow-water neritoideans, and the remaining less known neritopsines. All of known species of *Shinkailepas* have been described based chiefly on the shell, radula, operculum, and external morphology of the animal (Okutani et al., 1989; Beck, 1992; Warén & Bouchet, 2001; Sasaki et al., 2003), and only limited anatomical descriptions have been published for internal organs of the genus.

In this study, we attempted to provide detailed account of anatomical organization of *Shinkailepas myojinensis* by gross dissection, scanning electron microscopy, and histological serial sections. The results of observations are compared with existing knowledge of organ systems of other nertiopsines, and their significance is discussed in terms of comparative anatomy and systematics.

MATERIALS AND METHODS

Materials examined in this study were selected from part of paratype series of *S. myojinensis* and those preserved at the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). Details of sampling data are shown in the original description. Samples fixed in formalin were used for anatomical observations. After removed from the shell, soft parts of five specimens were dissected under a binocular microscope. Pieces of dissected soft parts were dried with a freeze-drier (Hitachi ES2030) and observed with SEM (Hitachi S2400). Whole animals of two females and three males were thin-sectioned at the thickness of 6 µm after embedding in paraffin. They were stained by a standard method of Mayer's Hematoxylin and Eosin staining. Whole series of sections (UMUT RM28647–28651) and SEM stub (UMUT RM28652) are deposited in the Department of Histological Geology and Paleontology, the University Museum, the University of Tokyo (UMUT). The terminology used in the descriptions chiefly followed that of Sasaki (1998) and Kano & Kase (2002).

RESULTS

Shell and Operculum

See Sasaki et al. (2003).

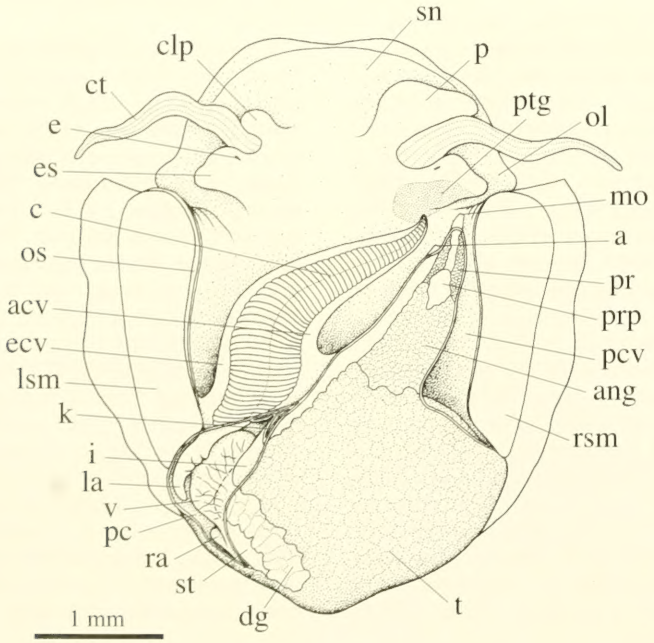

FIG. 1. Dorsal view of animal, male, with mantle removed.

External Anatomy

The animal is dorsoventrally flattened and symmetrical in outline. The visceral mass is not spirally coiled (Fig. 1). The dorsal surface of the animal is covered with a thin mantle. The entire surface of the mantle carries dense filamentous mantle processes (mp: Fig. 3A), which are multicellular and contain fiber-like structure internally (Fig. 4A). These processes are not branched and some of them penetrate through whole thickness of the shell at positions corresponding to the shell pores (cf. Sasaki et al., 2003: fig. 12C). The dorsal side of mantle margin also bears similar processes (Fig. 3B).

The mantle margin (mm: Figs. 2, 4C) is prominently thickened, divided into the outer and inner folds by the periostracal groove (pg: Figs. 3B, 4C). Its inside contains muscle fibers and blood sinus. The portion of the mantle covering the pallial cavity is provided with extensive blood sinus with numerous hemocytes inside (pls: Fig. 4F) and probably functions as a respiratory surface.

Major part of the ventral side of the animal is occupied by a circular, flattened pedal sole (ps: Fig. 2). Its anterior margin is marked by the anterior pedal groove (apg: Figs. 2, 4B) with the opening of the anterior pedal gland (apd: Fig. 4B). The ventral side of the head is extended as the oral lappet (ol: Figs. 2, 3C). The circumference of the mouth is thickened, papillate, and wrinkled (Fig. 3C). The lateral foot is smooth without any protrusive structure. The epipodial fold is extended between posterior dorsal rim of the foot and the mantle margin and provided with triangular tentacles (Figs. 2, 3D). The epipodial tentacles lack micropapillae, sense organ and ciliated structure. Their number ranges from 11 to 19, varying among specimens examined. The operculum is firmly attached to the dorsal surface of the foot musculature below the visceral mass.

The head consists of the snout, cephalic tentacles, cephalic lappets, and eye stalks (Fig. 1). The snout is stout, short and not tapered. The cephalic tentacles are paired in equal form and size, symmetrically positioned on each side of the head, not covered with sensory papillae, and striated by internal longitudinal muscle. The cephalic lappets are symmetrical, equal in size in female, but the right one is greatly enlarged in the male as the penis (p: Fig. 1). The eye stalks are posterior to the cephalic tentacles, flattened, and morphologically identical between both sexes. Only the posterior half of the right eye stalk is covered with a patch of tall glandular cells, which are here termed the "post-tentacular gland" (ptg: Figs. 1, 4F). Black eye spots are visible externally in anterior middle part of the eye stalks (Fig. 1).

The shell muscle is divided into right and left portions (lsm, rsm: Fig. 1), leaving separated scars on the internal surface of the shell. Each muscle is not subdivided into bundles, nor penetrated by blood vessels. The head retractor muscles are merged with shell muscles and do not produce independent attachment areas. The mantle is devoid of particular retractor muscle inserted on the shell, but instead attached to the shell by penetration of pallial processes.

Pallial Cavity

The pallial cavity is deep and attains the level of the posterior end of both shell muscle attachments. It contains the ctenidium, osphradium (os: Fig. 4E), anus, the kidney opening (ko: Fig. 10C), and genital opening(s).

The ctenidium is single, extended from the posterior left to the anterior right (Fig. 1). The ctenidial lamellae are bipectinate in alternating

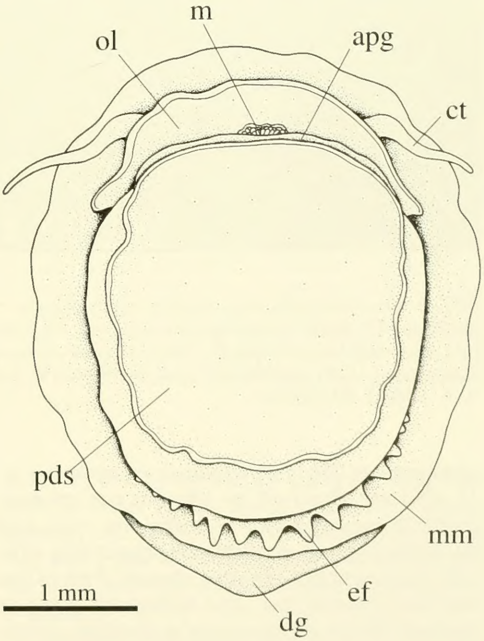

FIG. 2. Ventral view of animal.

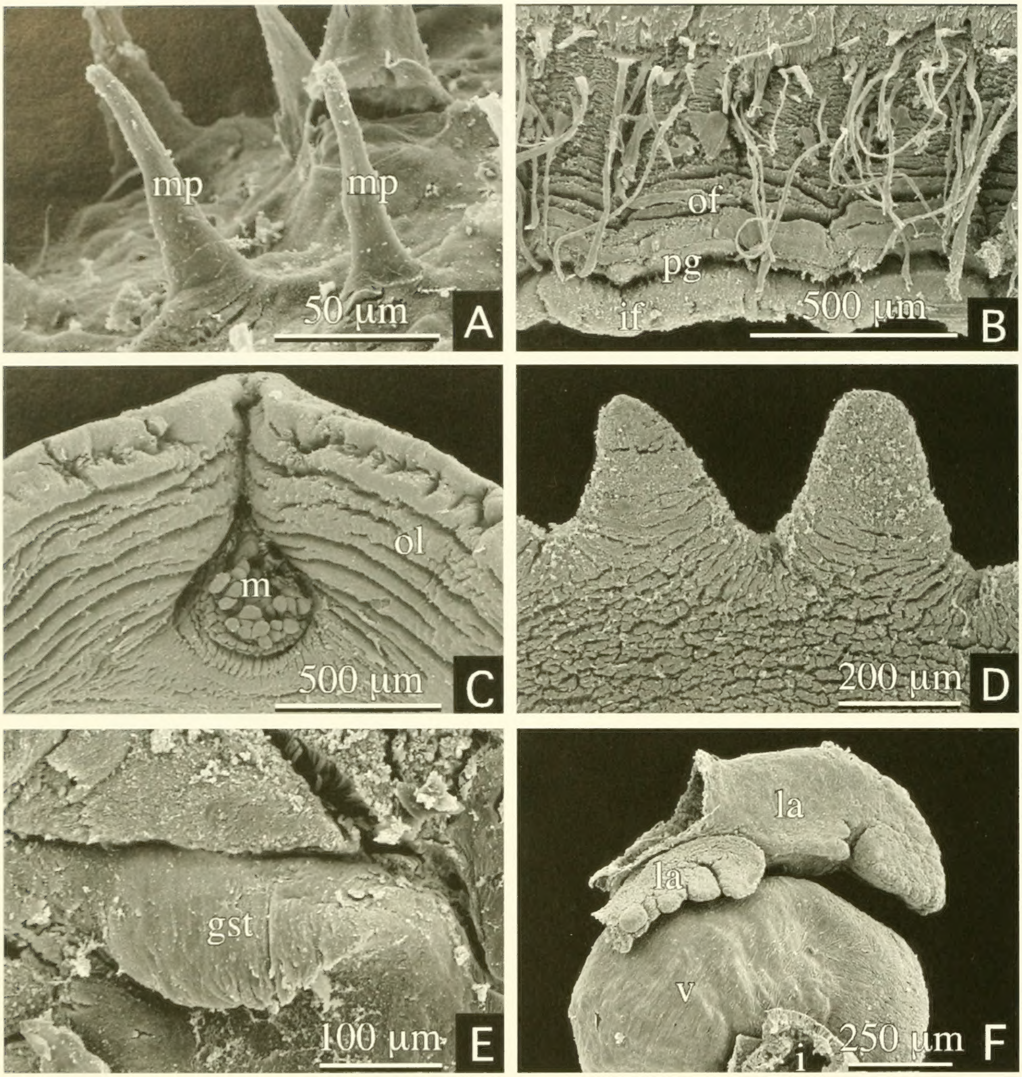

FIG. 3. Scanning electron micrographs of external and internal organs. A. Mantle processes (mp) on surface of mantle covering visceral part. B. Dorsal view of mantle margin. C. Ventral view of mouth (m) and oral lappet (ol). D. Ventral view of epipodial fold. E. Tooth of gastric shield (gst) inside of stomach. F. Left auricle (la) and ventircle (v) penetrated by intestine (i), removed from pericardium. A–F. UMUT RM28652.

arrangement (Fig. 4D), ridged along midline (Fig. 1), and not attached by afferent nor efferent ctenidial membranes. The skeletal rods and buriscles (sensory pockets) are absent (Fig. 4D).

A hypobranchial gland is absent. Part of the mantle opposing the post-tentacular gland is covered with a tall glandular epithelium, which is termed the "anterior pallial gland" (apl: Fig. 4F). This gland is also extended to cover the distal tip of the pallial gonoduct. Dorsoventrally paired, two glands, the post-tentacular gland on ventral side and the anterior pallial gland on dorsal side, are developed in the same position and size in both sexes. The epithelium of equivalent part on the left side is not specialized as gland.

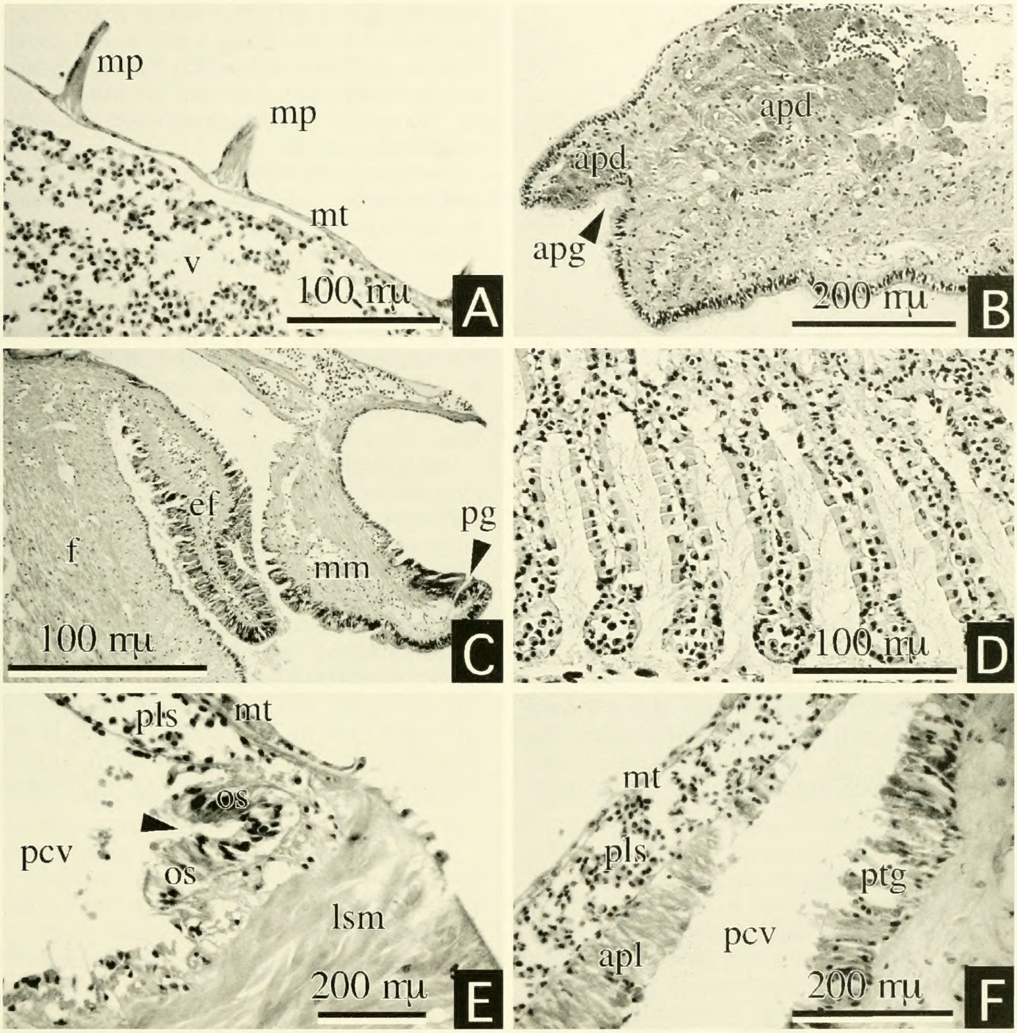

FIG. 4. Histology of external and pallial organs. A. Vertical section of mantle processes (mp) arising from mantle (mt) above ventricle (v). B. Longitudinal section of anterior tip of foot, showing anterior pedal gland (apd) and anterior pedal groove (apg). C. Longitudinal section of posterior part of foot (f) and mantle margin (mm). Epipodial fold (ef) arises from part of foot. D. Longitudinal section of ctenidial lamellae. E. Cross section of osphradium (os) along left shell muscle (lsm). Arrowhead indicates longitudinal groove on osphradium. F. Cross section of two opposing glands in pallial cavity near right eye stalk. A, E–F. UMUT RM28648. B–D. UMUT RM28651.

Digestive System

The digestive system consists of the oral tube, sublingual pouch, buccal cavity, buccal mass, radula, esophagus, stomach, digestive glands, and intestine to anus (Fig. 5).

The mouth opens ventrally (Fig. 1). The oral tube is considerably short in front of the buccal mass and followed by the sublingual pouch ventrally and by the buccal cavity dorsally. The anterior inner wall of the buccal cavity is particularly thickened as the transverse buccal fold with a pair of distinctly cuticularized plates (cp: Fig. 10). The jaw with tooth-like elements is absent.

The sublingual pouch is well developed below the buccal mass (slp: Fig. 7). Its epithelium is thin and smooth. Paired sublingual

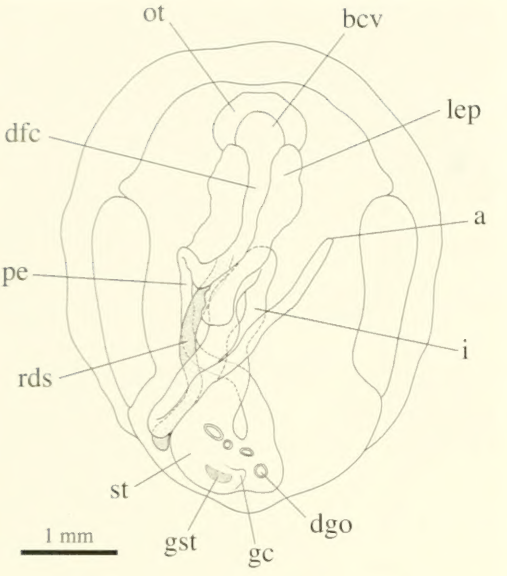

FIG. 5. Configuration of digestive tract in dorsal view.

glands project on each side of sublingual pouch and open into ventrolateral side of the oral tube (slg: Fig. 7). Their inner surfaces are roughened with irregular forms of glandular epithelium (Fig. 9B). The dorsal side of buccal cavity is thickened by a pair of well-developed dorsal folds (df: Fig. 9D). Salivary glands are not differentiated around the buccal cavity. The radular diverticulum is deep below the esophageal valve.

The buccal mass is elongated longitudinally and connected with body wall musculature with the lateral protractors (lp), inner and outer pairs of the ventral protractors (ivp, ovp), median and dorsal levators (ml, dl), posterior depressors (pd), anterior levators (al), and anterior tensors (at) (Figs. 6, 7). The posterior part of the odontophore is separated on both sides of radular sac and closely tied by postdorsal buccal tensor (pdt: Fig. 6) on the dorsal surface.

The buccal mass is internally supported by five odontophoral cartilages. The anterior cartilages are paired, elongated longitudinally, increasing in width backwards. The posterior cartilages are also paired, much smaller than the anterior pairs, firmly attached to the anterior pairs, and tapered posteriorly with pointed posterior ends. The median cartilage is unpaired, of almost the same length as the anterior cartilages, and lies between the anterior cartilages (Fig. 8). Its anterior one-fifth is demarcated by dorsal constriction and is smoothly swollen ventrally (Fig. 8). Ventral

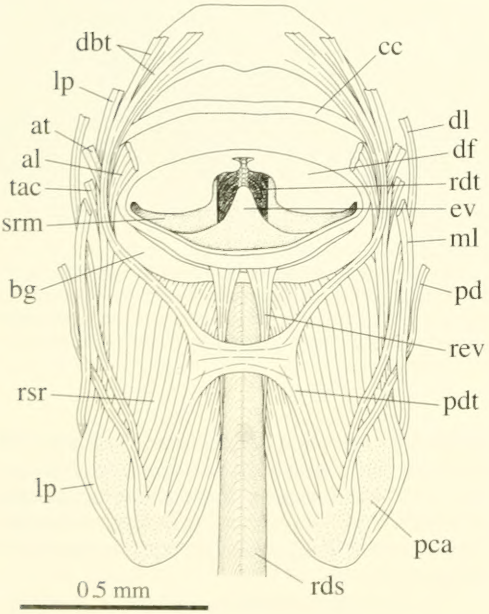

FIG. 6. Drosal view of buccal mass, with anterior digestive tract intact.

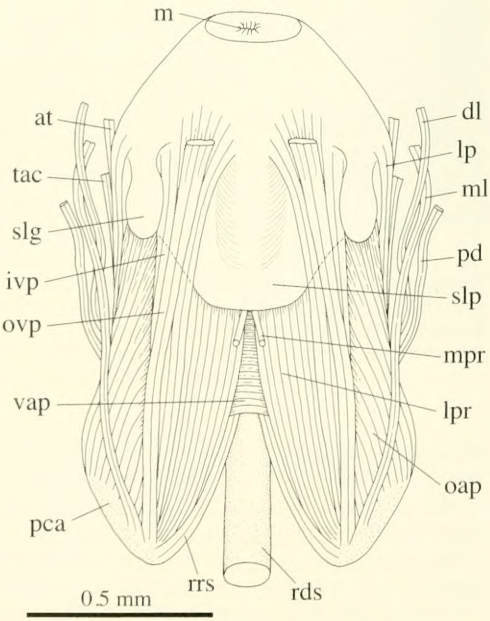

FIG. 7. Ventral view of buccal mass, with oral tube and sublingual pouch intact.

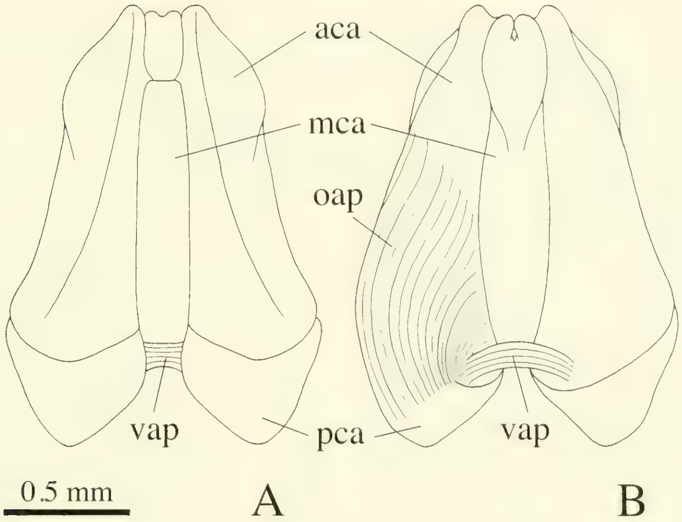

FIG. 8. Odontophoral cartilages. A. Dorsal view. B. Ventral view. Outer approximator muscle (oap) is removed on left side. Anterior part of ventral approximator muscle (vap) is also removed (cf. Fig. 7).

sides of the anterior cartilages are connected by the ventral approximator muscle (vap: Fig. 7). The anterior and posterior cartilages are longitudinally united with the outer approximator muscles (oap: Fig. 7). Sides of anterior cartilages are attached to the body wall by tensor muscles (tac: Figs. 6, 7).

The radula is composed of an ensheathed part of the radular sac posterior to the buccal cavity, the subradular membrane spread over the buccal mass, and functional area exposed into the buccal cavity on the bending plane. The radular sac is extended backwards and not coiled in loops. Its posterior end is smooth and simple. The subradular membrane is attached by the median and lateral protractor muscles (mpr, lpr: Fig. 7) anteriorly, and the retractor muscles (rsr: Fig. 7) laterally and posteriorly. The retractor muscles of radular sac (rrs: Fig. 7) originate from the posterior end of the posterior cartilages, insert on the radular sac ventrally. The radular teeth morphology was described by Sasaki et al. (2003).

The esophagus begins from the posterodorsal part of the buccal mass and comprises two parts, the anterior and posterior esophagi. The anterior esophagus is dorsoventrally depressed, almost consistent in width and curves towards the left over the buccal mass. Inside of the anterior esophagus is divided into the dorsal food channel (dfc) in the center and the lateral esophageal pouches (lep) on both sides by a pair of the dorsal folds (Figs. 9D, E). The inside of the lateral esophageal pouches is glandular, and therefore, it can also be called the anterior esophageal gland. Behind the buccal mass, a main part of the anterior esophagus slightly turns forward to form a very short loop. The posterior part of lateral oesphageal pouches are separated from dorsal food channel, extending ventrally as the posterior esophageal gland, and surrounds the radular sac completely (peg: Fig. 9F). Their epithelia are heavily folded (Fig. 9F). The posterior esophagus is narrower than the anterior esophagus (Fig. 5), and defined by corrugated inner structure (Fig. 9G). It runs below the radular sac and other organs at the deepest level of the visceral cavity.

The stomach is marked by the enlargement in diameter and folded into U shape. The inside has large cuticularized area, short crescent-shaped gastric caecum (gc: Fig. 5), tooth of gastric shield (gst: Figs. 3E, 5), and paired typhlosoles on the ventral side. The digestive glands are well developed around the stomach and connected to the distal part of the stomach through four openings dorsally and two openings ventrally. The ducts of digestive glands are further divaricated complicatedly.

The intestine is circular in cross section, nearly consistent in diameter along its entire length, turns in two sites, posterior to the buccal mass and below the pericardium (Fig. 5).

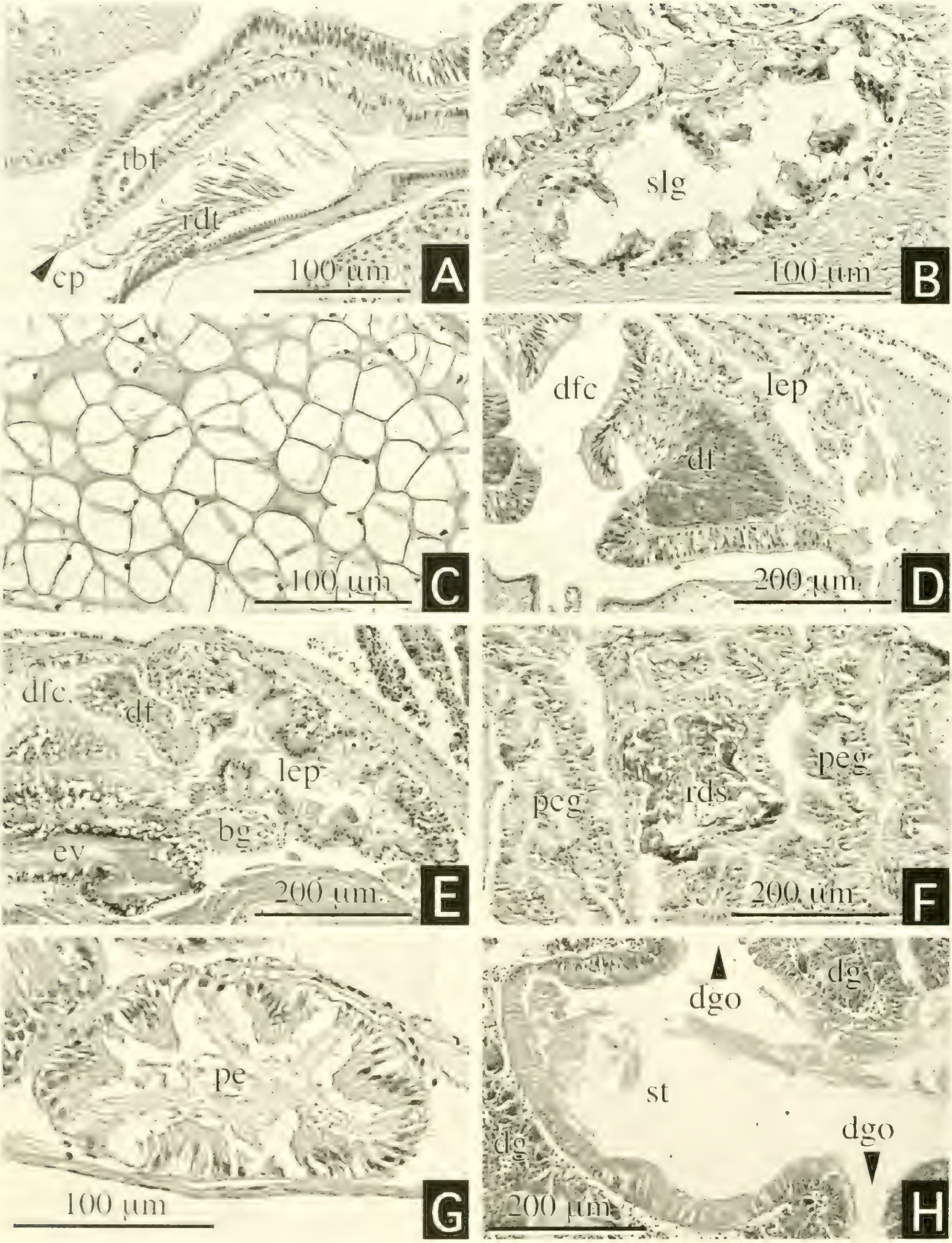

FIG. 9. Histology of digestive system. A. Longitudinal section of transverse buccal fold (tbf), cuticularized plate (cp), and radular teeth (rdt). B. Cross section of sublingual gland (slg). C. Vertical section of anterior odontophoral cartilage. D. Cross section of left half of dorsal fold (df) and lateral esophageal pouch (lep) over anterior part of buccal mass. E. Cross section of left half of anterior esophagus in more posterior part than in Fig. D. F. Cross section of posterior esophageal gland (peg) surrounding radular sac (rds). G. Cross section of posterior esophagus (pe). H. Cross section of stomach, showing openings to digestive glands (dgo) on dorsal and ventral (upper and lower in figure) sides. C, H. UMUT RM28647. B, D–F. UMUT RM28648. A, G. UMUT RM28651.

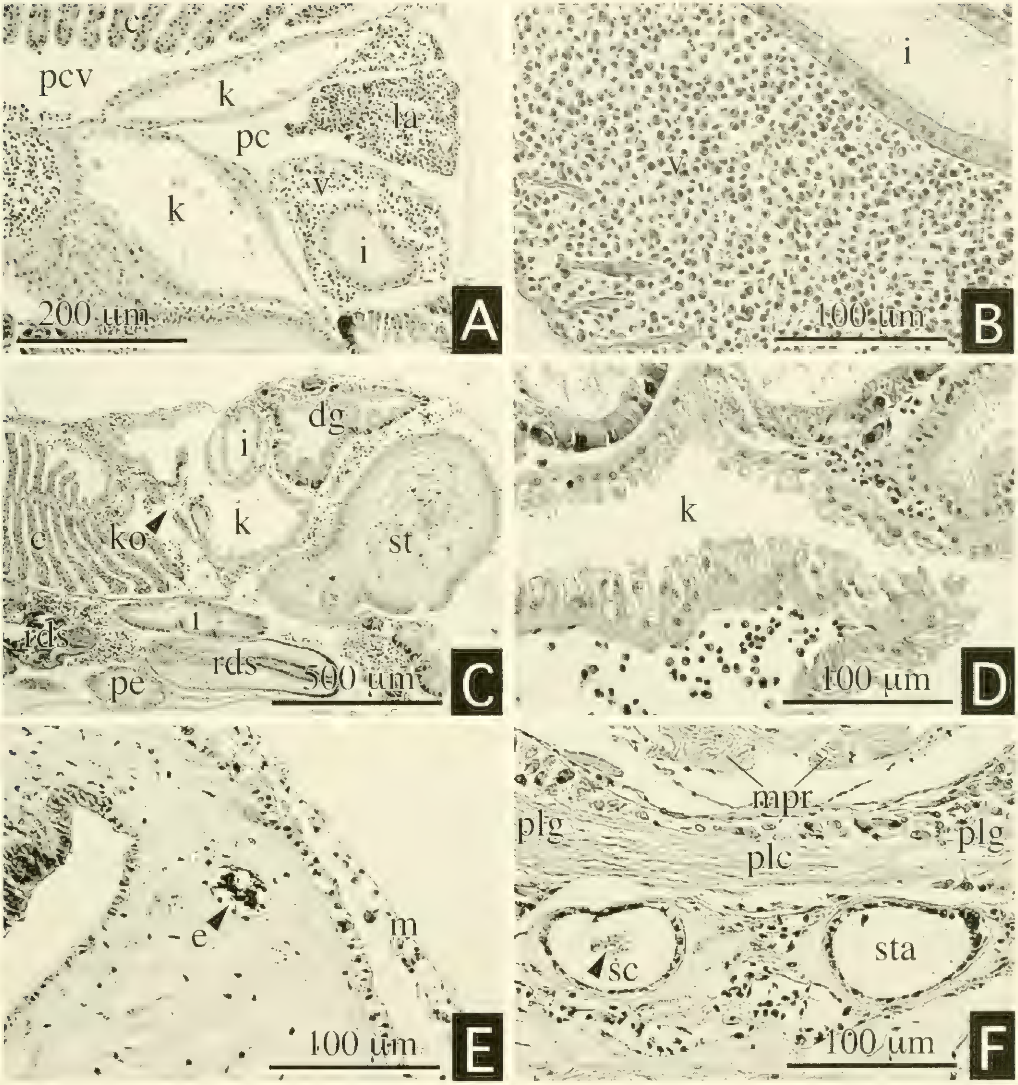

FIG. 10. Histology of circulatory and excretory systems and sense organs. A. Horizontal section of kidney (k) and pericardium (pc). B. Enlarged view of ventricle (v) penetrated by intestine (i). C. Longitudinal section of kidney (k), its opening (ko) and adjacent organs. D. Enlarged view of epithelium of kidney (k). E. Cross section of left eye (e). F. Cross section of statosysts (sta) containing statoconia (sc) below pleural commissure (plc). D. UMUT RM28647. E–F. UMUT RM28648. A–C. UMUT RM28651.

Its epithelium is densely ciliated and composed of a layer of prismatic cells (Fig. 10B). Around the second turn, the intestine penetrates the ventricle and the pericardium. No anal (rectal) gland was found near the distal part of the intestine. The anus opens on the right anterior side of the pallial cavity (Fig. 1).

Circulatory System

The heart is enclosed in the pericardium and consists of paired auricles of unequal size and a median ventricle (Figs. 1, 3F, 10A). The left auricle is much larger than the right and connected to blood vessels from the ctenidium and

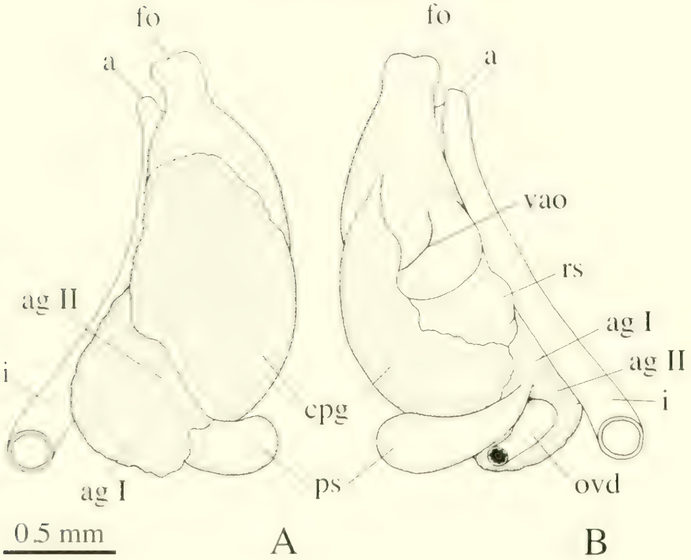

FIG. 11. Pallial oviduct of female, with intestine intact. A. Dorsal view. B. Ventral view.

the mantle. The margin of the left auricle is rugose and constricted to be separated into a few chambers (Fig. 3F). The right auricle is vestigial and situated posterior to the ventricle (Fig. 1). The ventricle is voluminous, penetrated by the intestine, stiffened by cardiac muscles inside (Fig. 10B). An aorta from the ventricle is short and opens into haemocoel of the body. An aortic bulb is not formed. Large sinuses are developed among visceral organs and around the buccal mass. Considerable blood sinuses are also found near the lateral wall of the pedal musculature. Blood space adjacent to the kidney is connected anteriorly to the afferent ctenidial vessel.

Excretory System

The excretory organ consists of a single kidney and the pericardium. The kidney is on the posterior side of the ctenidium; its excretory opening is located below ctenidial base (ko: Fig. 10C). The inside of the kidney is partly partitioned into two branches on the anterior and right sides of the pericardium, respectively (Fig. 10A), but both are indistinguishable in histology. The epithelium of the kidney is not lamellated throughout the entire area and consists of single-layered papillate cells with basal nuclei (Fig. 10D). The renopericardial connection is extended between the two branches of the kidney.

Reproductive System

The sexes are separate, and their reproductive organs exhibit striking sexual dimorphism. Large part of the reproductive organ is occupied by the gonad and pallial gonoduct. In both sexes, the gonad develops dorsal to the digestive gland, the gonoduct is not connected to the kidney, and gonopericardial connection is not present.

The female reproductive system consists of the ovary, a thin oviduct connecting the ovary and the pallial oviduct, a complex of pallial oviduct and associated glands, and the vaginal duct. The ovary and dorsal surface of the pallial oviduct are visible on the dorsal side of the animal through the mantle. The oviduct is thin and circular in cross section, arises from anteroventral part of the ovary, extends forward, and enters the pallial oviduct from its ventral side (Figs. 11B, 12, 15C).

The pallial oviduct is surrounded by two differently stained glands, a posteriorly situated albumen gland, and an anteriorly located capsule gland. The albumen gland covers posterior area of the pallial oviduct and is further subdivided into two portions, albumen gland I and II (agI, agII: Fig. 11). Both parts are not stained darkly, and the albumen gland I is obviously more translucent than the albumen gland II (Fig. 15C). The pallial oviduct opens into the pallial cavity through its anterior tip (fo: Fig. 11).

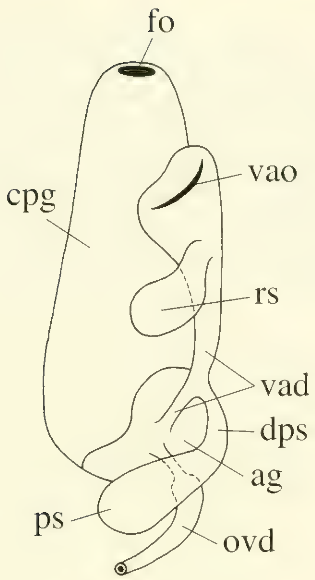

FIG. 12. Schematic drawing of ventral view of pallial oviduct, showing connection of various ducts and associated structures.

The vaginal duct is ventral to the pallial oviduct, covered entirely with epithelium of pallial oviduct, elongated, and connected to the pallial oviduct posteroventrally. The terminal of the vaginal duct is expanded and opens as an oblique slit (vgo: Fig. 11B). Posterior to the vaginal opening, the receptaculum seminis is branched off from the vaginal duct. Spermatozoa are oriented in the receptaculum seminis towards its epithelium (Fig. 15A). The distal end of the receptaculum seminis is visible in ventral view (Fig. 11B). Near its connection to the pallial oviduct, the vaginal duct gives off another pouch-like structure. It is tentatively named “posterior sac” because of unknown function and uncertain homology with other reproductive structures. Its inside is characteristically roughened by many folds (ps: Figs. 15B–E), and no spermatozoa was found there. A groove or ovipositor is not developed on the right side of the neck of the female.

The male reproductive organ is composed of the testis (Fig. 15F), vas deference, seminal vesicle, and pallial male gonoduct (Fig. 13). The testis contains many cylindrical sectors in which growing sperms are arranged radi-

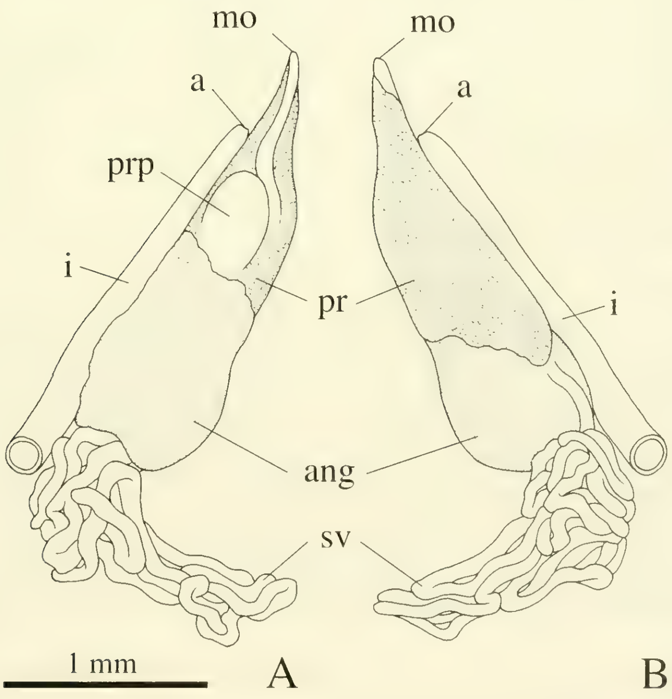

FIG. 13. Pallial gonoduct of male, with intestine intact. A. Dorsal view. B. Ventral view.

ally. A thin vas deference originates from the ventroanterior side of the testis and extends anteriorly. The distal part of the vas deference is complicatedly folded to form the seminal vesicle. which is filled with filamentous. completed spermatozoa oriented in parallel (Figs. 14C–D, 15G). The spermatophore was not observed in any section of vas deference.

The pallial male gonoduct is greatly enlarged and surrounded by two different glands, the annex gland posteriorly and the prostate gland anteriorly (Figs. 13, 15H). In dorsal view, a part of the prostate pouch is visible on the outer surface (Fig. 13A).

The penis arises from inner side of right cephalic tentacle, dorsoventrally depressed, lobate with a tapered tip (Fig. 1). Its dorsal surface is smooth, the right margin is grooved throughout, and the ventral side has a single ciliated papilla (Figs. 14A, B). A ciliated groove was not found between the gonoduct opening and the penis.

Nervous System

The nervous system consists mainly of the circumesophageal nerve ring, pedal cords, and visceral nerve. The circumesopahgeal nerve ring is formed by pairs of three major ganglia, namely, pleural, pedal, and cerebral ganglia. Their configuration is of hypoathroid type, namely pleural and pedal ganglia are more adjacent than cerebral ganglia (Fig. 16).

The cerebral ganglia are located on the bases of the cephalic tentacles and send nerves to the cephalic tentacles and oral area. The paired ganglia are connected to each other by the cerebral commissure over the oral tube and the labial commissure below the sublingual pouch. Labial ganglia are not formed on the labial commissure. The buccal ganglia are obliquely extended at the base of the anterior esophagus and connected to the cerebral ganglia through thin connectives.

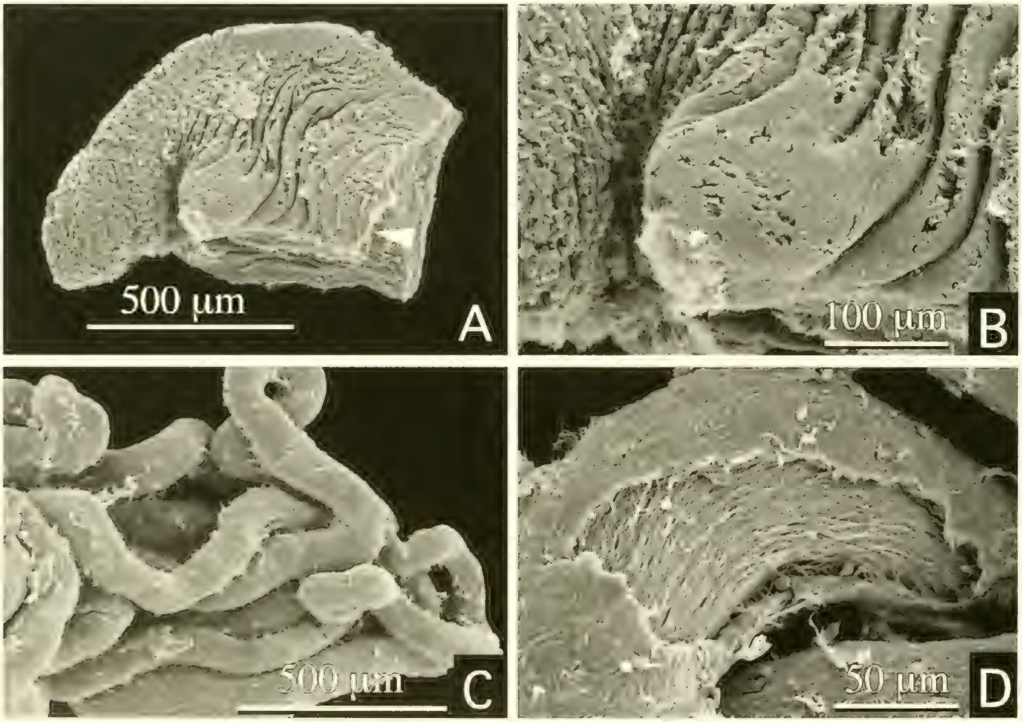

FIG. 14. Scannning electron micrographs of male reproductive organs. A. Ventral view of penis removed from head. Arrowhead indicates groove along right margin. B. Enlarged view of ciliated papilla on right ventral side. C. Seminal vesicle in convoluted part of vas deference. D. Spermatozoa contained in seminal vesicle. Part of epithelium of seminal vesicle is removed to show inside. A–D. UMUT RM28652.

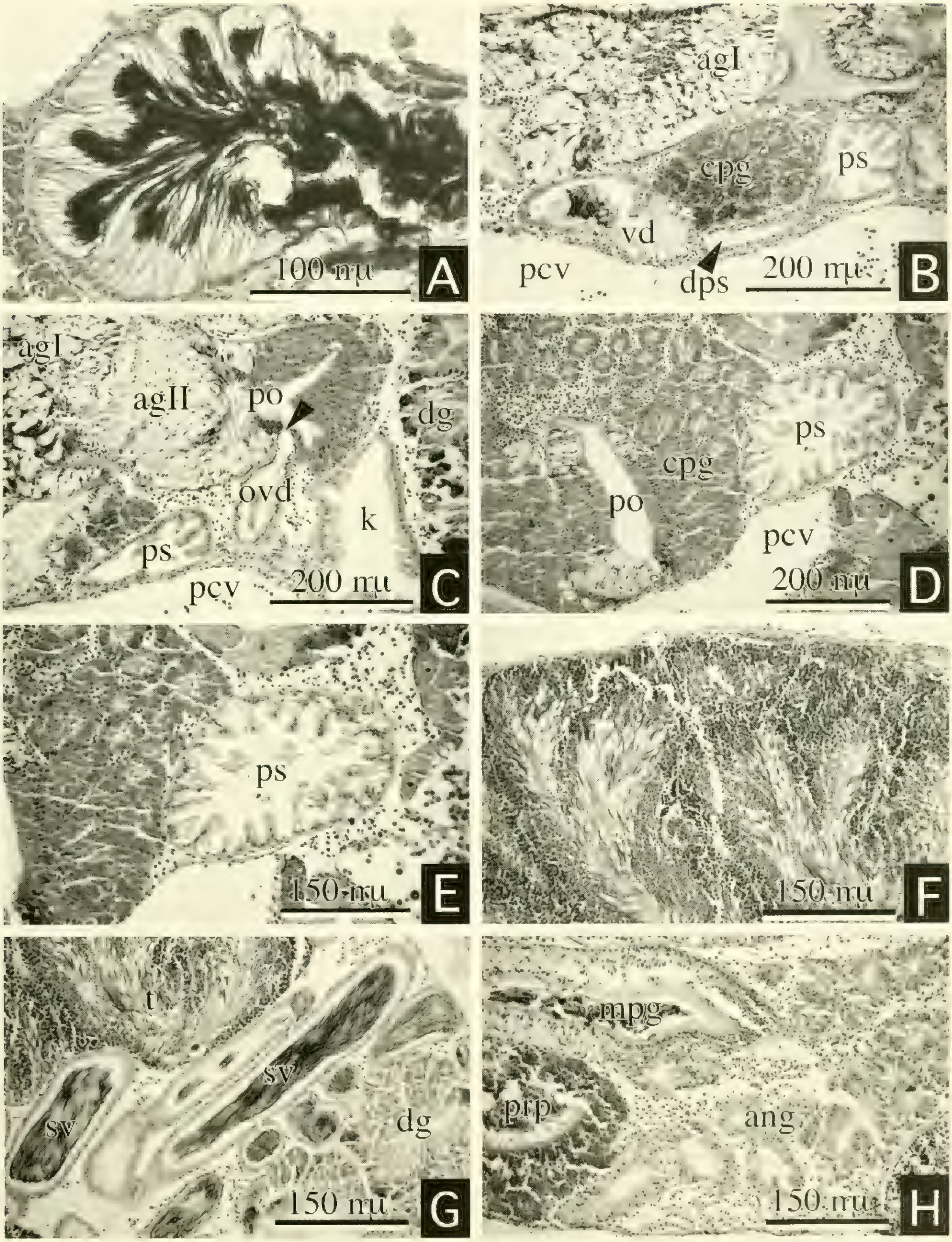

FIG. 15. Histology of reproductive organs of female (A–E) and male (F–H). A. Cross section of seminal receptacle. B. Longitudinal section of posteroventral part of pallial oviduct. C. Longitudinal section of pallial oviduct where oviduct (ovd) is connected to lumen of pallial oviduct. D. Longitudinal section of posterior sac (ps) of vaginal duct and surrounding glands. E. Enlarged view of longitudinal section of posterior sac (ps) of vaginal duct. F. Vertical section of testis. G. Vetical section of seminal vesicle (sv) containing completed spermatozoa. H. Horizontal section of glands of pallial gonoduct of male. A. UMUT RM28648. F–H. UMUT RM28650. B–E. UMUT RM28651.

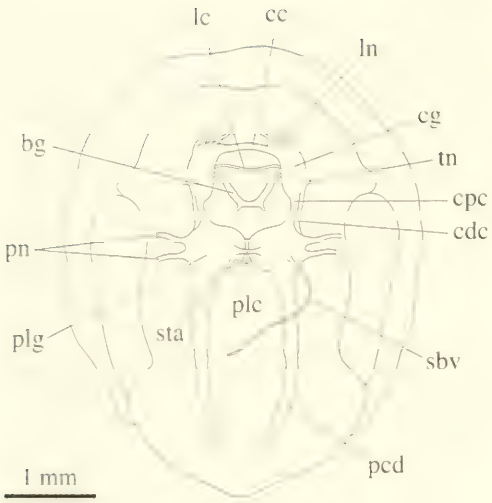

FIG. 16. Configuration of nervous system in dorsal view.

The pleural ganglia are situated below the posterior part of the buccal mass, and they are the largest among all ganglia and connected by a rather thin pleural commissure. Two distinct nerves are extended from the pleural ganglia to the body wall musculature.

The pedal ganglia underlie pleural ganglia and are connected by the pedal commissure. The pleural and pedal ganglia are juxtaposed closely, forming almost fused complexes, but they receive separate cerebropleural connectives and cerebropedal connectives, respectively, from the cerebral ganglia. The pedal ganglia give off thin nerves anteriorly and thick pedal cords posteriorly. Pedal cross connection was not detected in the present sections.

The visceral nerve is not a closed loop or streptoneurous and represented only by the subesophageal part, which arises from the right pleural ganglion toward base of ctenidium along the pallial cavity wall. The supraesophageal part is totally missing.

Sense Organs

Possible sensory organs include cephalic tentacles, oral lappets, papillae on the outer lip of the mouth, posterior epipodial fold, osphradium, statocysts, and eyes. The most of external structures are described above. Epipodial sense organs, and subradular organs are absent.

The osphradium is elongated as a vermiform ridge along the left shell muscle, weakly developed, and two-folded with a longitudinal central groove (os: Fig. 4E). Eyes are rudimentary without cornea and lens, simply represented by pigmented cells, and sunken in connective tissue of eye stalks. Statocysts are attached to the dorsal side of pedal ganglia and below pleural commissure (plc: Fig. 10F) and contain several statoconia (sc: Fig. 10F).

DISCUSSION

Comparative Morphology

The morphology of neritopsine gastropods, in which *Shinkailepas* is included, is highly diverse in both shell and soft parts. Their similarity and dissimilarities have been employed for systematics at various taxonomic levels (e.g. Sasaki, 1998) and also used as characters for phylogenetic analysis (Ponder & Lindberg, 1997; Sasaki, 1998). The results of observations on *Shinkailepas myojinensis* in this study are compared with descriptions of relatively well-investigated genera (Tables 1, 2).

Shell: The shell of *Shinkailepas* is characterized by (1) a limpet form with the apex on the posterior center, (2) a multispiral globular protoconch with growth lines, (3) the septum extended between the visceral mass and foot, and (4) microscopic canal structures with crowded openings inside and sparse outside. Among these, (1) and (3) are also found in *Phenacolepas* and *Septaria*. (2) is shared by aquatic neritopsines in general (Sasaki, 1998). The shell of another vent-associated neritopsine limpet, *Olgasolaris*, differs from that of *Shinkailepas* in a more centrally situated apex, many regular and fine radial riblets, and thick periostracum overhanging the shell margin. *Phenacolepas* and related shallow-water forms are most similar to *Shinkailepas* among Neritopsina in above characters, except (4).

It is well known that numerous thin canals and corresponding pores are produced independently in the shells or valves of all polyplacophorans, part of bivalves and gastropods, and brachiopods (reviewed by Reindl & Haszprunar, 1996). In Gastropoda, canals and mantle processes (caeca) are found in the Fissurellidae (Reindl & Haszpruanr, 1994), Neritiliidae (Kano & Kase, 2002), *Shinkailepas* (Beck, 1992; Sasaki et al., 2003; this study), and *Olgasolaris* (Beck, 1992). Shell canals of *Shinkailepas* (and possibly also *Olgasolaris*)

TABLE 1. Comparison of character states in *Shinkailepas* and non-phenacolepadid neritopsine genera.

Family	Phenacolepadidae	Neritiliidae	Neritidae	Neritidae	Helicinidae
Genus	*Shinkailepas*	*Pisulina, Neritilia*	*Septaria*	*Nerita*	*Waldemaria*
Reference	this study	Kano & Kase (2002)	Sasaki (1998)	Sasaki (1998)	Sasaki (1998)
shell form	limpet	coiled	limpet	coiled	coiled
canal structures of shell	partly penetrating shell completely	opening only inside of shell	absent	absent	absent
operculum shape	trapezoidal	semicircular	trapezoidal	semicircular	semicircular
apophysis of operculum	absent	present	present	present	absent
epipodial flap	present	absent	absent	absent	absent
cephalic lappet	present	absent	absent	absent	absent
ctenidium	well-developed	vestigial	well-developed	well-developed	absent
vestigial gill on right side	absent	absent	absent	present	absent
hypobranchial gland	absent	present	present	present	present
anterior pallial gland	present	?	?	?	?
post-tentacular gland	present	?	?	?	?
sublingual gland	present	present	present	present	absent
central tooth of radula	present	absent	present	present	present
lateral teeth of radula	fourth teeth longitudinal	outer (third) teeth oblique	fourth teeth transversely shield-like	fourth teeth transversely shield-like	fourth teeth oblique
lateromarginal plate	absent	present	absent	absent	absent
radular sac	short	long	short	short	short
anterior esophageal glands	not elongated	elongated posteriorly	not elongated	not elongated	not elongated
floor gland in anterior esophagus	absent	present	absent?	absent?	absent?
posterior esophageal glands	tightly enclosing radular sac	loosely enclosing radular sac	lateral to radular sac	lateral to radular sac	lateral to radular sac

(continues)

(continued)

Family	Phenacolepadidae	Neritiliidae	Neritidae	Neritidae	Helicinidae
Genus	*Shinkailepas*	*Pisulina, Neritilia*	*Septaria*	*Nerita*	*Waldemaria*
Reference	this study	Kano & Kase (2002)	Sasaki (1998)	Sasaki (1998)	Sasaki (1998)
opening(s) between stomach and digestive glands	paired	single	paired	paired	paired
glandular and non-glandular regions of kidney	undifferentiated	undifferentiated	differentiated	differentiated	differentiated
right auricle	present	present	present	present	absent
erythrocytes	possibly present	absent	absent	absent	absent
female reproductive openings	diaulic	diaulic	triaulic	diaulic	diaulic
vaginal opening	slit-like, anterior	slit-like, posterior	small pore, anterior	small pore, anterior	small pore, posterior
receptaculum seminis	posterior to vaginal opening	part of spermatophore sac	connected to dorsal albumen gland	connected to dorsal albumen gland	absent?
posterior sac of vaginal duct	present	absent	absent	absent	absent
crystal sac in female	absent	absent	present	present	absent
neck furrow in female	absent	present	absent	absent	absent
female flap	absent	present	absent	absent	absent
seminal vesicle	entangled	double, uncoiled	entangled	entangled	simple
cephalic penis	present	rudimentary or absent	present	present	absent
seminal groove on penis	lateral	?	?	?	-
visceral nerve loop	incomplete	incomplete	complete	complete	complete?
eyes	vestigial, closed	vestigial, open	well-developed, closed	well-developed, closed	well-developed, closed
osphradium	present	present	present	present	absent
central zone of osphradium	longitudinally grooved	?	?	simple	-
statocyst position relative to pedal ganglia	posterodorsal	anterior	posterodorsal	posterodorsal	posterodorsal
statocyst content	statoconia	statolith	?	?	?

are different from those of above-mentioned taxa in two points: (1) The diameter, cross-sectional form, and density of the canals are more prominently variable in *Shinkailepas* (Sasaki et al., 2003: fig. 12C), and (2) some of canals penetrate the shell completely, but many of them do not. In the Fissurellidae, all canals penetrate the shell at least in an early ontogenetic stage with a rather constant diameter (e.g., Sasaki, 1998: fig. 40d). In the Neritiliidae, canals never reach the outer surface of the shell (Kano & Kase, 2002). Similar canals are not found in any section of the shell in other neritopsines, such as *Nerita* and *Cinnalepeta* at microstructural level (Sasaki, 2001).

Operculum: Most neritopsines are operculate, except the Ceresidae, Proserpinidae (Thompson, 1980) and shell-less *Titiscania*. The common features of the opercula of *Shinkailepas* (and *Olgasolaris*) include (1) its position on the foot musculature below the visceral mass, (2) a trapezoidal, nail-like shape in outline, (3) two-layered structure, namely, calcified and corneous parts, (4) the nucleus located on the left side relative to animal's longitudinal axis, (5) the division into initially spiral and subsequently non-spiral parts, possibly of pre- and post-metamorphic stages, by different modes of growth line formation, and (6) the absence of an apophysis (Okutani et al., 1989: fig. 12; Beck, 1992: pl. 1, fig. 4, pl. 5, fig. 4; Sasaki et al., 2003: fig. 12D). Among neritopsines, the opercula of *Shinkailepas* and *Olgasolaris* are most similar to that of *Septaria* in (1) and (2), but different in the remaining features. The demarcation of nucleus (possibly of pre-meta-

TABLE 2. Comparison of character states among four phenacolepadid genera.

Genus Reference	*Shinkailepas* this study	*Olgasolaris* Beck (1992)	*Phenacolepas* Fretter (1984)	*Cinnalepeta* Sasaki (1998)
canal structures of shell	partly penetrating shell completely	penetrating shell	absent	absent
operculum shape	trapezoidal	subtrapezoidal	semicircular, vestigial	absent
apophysis of operculum	absent	absent	?	-
circumpallial microtentacles	absent	absent	present	present
epipodial flap	present	present	absent	absent
cephalic lappet	present	present	absent	absent
posterior esopahgeal glands	tightly enclosing radular sac	?	lateral to radular sac?	lateral to radular sac
intestine	2 loops	2 loops	3 loops?	5 loops
glandular and non-glandular regions of kidney	undifferentiated	?	differentiated	differentiated
erythrocytes	spherical?	?	biconcave	biconcave
vaginal opening	transversely slit-like, anterior	transversely slit-like, anterior	small pore	small pore, anterior
receptaculum seminis	posterior to vaginal opening	?	present	connected to dorsal albumen gland
posterior sac of vaginal duct	present	?	absent	absent
female flap	absent	present?	present as ovipositor?	absent?
seminal groove on penis	lateral	dorsal	?	?
eyes	vestigial, closed	?	well-developed, closed	well-developed, closed

morphic part) is also known in the Neritiliidae (Kano & Kase, 2000, 2003, in press; Kano et al., 2003), *Bathynerita* (Warén & Bouchet, 1993), and *Phenacolepas* (Kimura & Kimura, 1999: fig. 7C–D), and therefore it is not characteristic of *Shinakailepas* and *Olgasoralis*. The possession of apophysis in the operculum is rather common throughout neritopsines except the Helicinidae, *Shinkailepas*, and *Olgasolaris* (cf. Sasaki, 2001). The number of microstructual layers varies from two to four in neritopsine opercula (Suzuki et al., 1991; Sasaki, 2001), but its phylogenetic or adaptive significance is uncertain.

External Anatomy: The mantle margin is normally simple without projective or massive glandular structure in neritopsines, but it is modified in shallow-water phenacolepadids. The inner fold of the mantle margin is characteristically fringed with retractile microtentacles in *Phenacolepas* and *Cinnalepeta* (Fretter, 1984: fig. 5; Sasaki, 1998: fig. 85b). In addition, a thick layer of glandular tissue is developed on ventral surface in *Phenacolepas* (Fretter, 1984: fig. 5). But, in contrast, such a specialization does not occur in *Shinkailepas*. The mantle margin morphology is, therefore, a distinctive character between shallow-water and deep-water phenacolepadids.

Various forms of folds or tentacles are developed in gastropod epipodium as in vetigastropods, cocculinifom limpets, "vent-taxa," deep-sea phenacolepadids, and part of cerithioideans (Ponder & Lindberg, 1997). In *Shinkailepas* and *Olgasolaris*, the epipodial fold arises from the latero- to postero-dorsal part of the foot in *Shinkailepas* (Okutani et al., 1989; Beck, 1992; Warén & Bouchet, 2001: fig. 33; this study), whereas comparable structure is totally absent in other neritospines including shallow-water phenacolepadids (Tables 1, 2). Because the degree of epipodial fold development is different from species to species, it is a useful taxonomic character at species level in *Shinkailepas* (see below).

The cephalic lappets are small flaps projected on the inner side of the cephalic tentacles. They are found in part of the vetigastropods and neritopsines and may be all regarded as homologue in terms of position and innervation. It is a common feature that the lappets are enlarged and used as a penis in male in neritopsines if present. The cephalic lappets are present in *Shinkailepas* (Fig. 1; Okutani et al., 1989: fig. 10), *Olgasolaris*, and *Bathynerita* (Warén & Bouchet, 2001), but absent in the Neritiliidae, shallow-water phenacolepadids, and the Neritidae excluding *Bathynerita* (Table 1).

Pallial Organs: The pallial cavity of *Shinkailepas* contains a set of pallial organs common to the aquatic Neritopsina, namely the ctenidium, osphradium, anus, pallial gonoduct with genital opening(s), and excretory pore, but a hypobranchial gland is absent.

The ctenidium of *S. myojinensis* has typical neritopsine elements: (1) a single ctenidium is situated on the left side, (2) ctenidial lamellae are bipectinate in opposing arrangement on either side of ctenidial axis, (3) ctenidial lamellae are centrally ridged, (4) skeletal rods and (5) sensory pockets are absent. These features are not distinguishable from those of other neritopsines, except for a greatly reduced ctenidium of the Neritiliidae (Kano & Kase, 2002) and its total absence of in terrestrial groups. A wart-like structure termed "vestigial gill" on the right side of the pallial cavity (Fretter, 1965: fig. 1c; Sasaki, 1998: fig. 77c) is lacking in *S. myojinensis*. The occurrence of the structure is restricted to members of the genus *Nerita* and not universal to neritopsines.

The hypobranchial gland is present on the right pallial roof in some neritopsines, for example, the Neritidae (Fretter, 1965; Berry et al., 1973; Sasaki, 1998), Neritiliidae (Kano & Kase, 2002), and Helicinidae (Thompson, 1980; Sasaki, 1998). However, it is absent in corresponding position in *S. myojinensis*, *Phenacolepas* (Fretter, 1984), and *Cinnalepeta* (Sasaki, 1998).

In *S. myojinensis*, two glandular zones (the post-tentacular gland and anterior pallial gland) are observed on the right anterior corner of the pallial cavity. These glands may be analogous to the hypobranchial gland of other gastropods, but probably do not fulfill the function as a normal hypobranchial gland due to their restricted position at the anterior right. The true hypobranchial gland develops in deeper position in the pallial cavity in other neritoideans. The two glandular zones in *S. myojinensis* possibly have a function related to reproduction, since the glands are developed near the gonoduct opening in both sexes.

Digestive System: Its has been generally accepted that neritopsines lack true jaws (Fretter, 1965). However, paired cuticularized plates apparently develop on the inner wall of the oral tube in *S. myojinensis* (Fig. 9A). Identical plates are also present generally in other neritopsines. Sasaki (1998) described these plates as jaws, because they are located at a position corresponding to those of other gastropods. They may not be regarded as the jaws in that they lack scaly microelements, but such microelements are also lacking in the jaws of *Cocculina* and Patellogastropods (Sasaki, 1998). Although the term "jaw" was not used in the present description, it is also possible that they represent a reduced state of the jaws. Homology can be established between jaws and cuticularized plates under positional criterion but is uncertain under structural criterion. More extensive comparison should be made among gastropod jaws for further discussion.

Buccal mass structure is remarkably useful character to define higher taxa in basal groups of gastropods (Sasaki, 1998). For example, patellogastropods, vetigastropods, and neritopsines each have their own composition of musculature and cartilages. The buccal musculature of *Shinkailepas* belongs to neritoidean type described for *Nerita, Septaria,* and *Cinnalepeta*, and is partially different from that of *Waldemaria* (Sasaki, 1998: table 5).

The configuration of odontophoral cartilages is invariable throughout the Neritopsina (Sasaki, 1998; Kano & Kase, 2002). Large anterior and small posterior cartilages are paired and connected by ventral approximator muscle, and the median cartilage is situated between the anterior cartilages. The structure of odontophoral cartilages of *S. myojienensis* conforms entirely to this pattern.

The presence of a pair of sublingual glands beside the sublingual pouches is a distinctive character of neritoideans, including the Neritidae, Neritiliidae, and Phenacolepadidae (Sasaki, 1998: Kano & Kase, 2002). They are absent in the Helicinidae (Sasaki, 1998) or unknown in the rest of neritopsine members. The salivary glands are absent throughout the Neritopsina without exception. Probably their absence is compensated by the development of sublingual glands and anterior esophageal glands.

The radular formula of *Shinkailepas* is the same as that of most members of neritoideans. The radula of *Shinkailepas* and that of *Olgasolaris* (Beck, 1992) are typified by the following six features: (1) the central tooth is present, (2) the first lateral teeth are obliquely elongate, (3) the second and third lateral teeth are small, (4) the fourth lateral teeth are longitudinally elongate without serration in their cusps, (5) lateromarginal plates are absent, and (6) the marginal teeth have small triangular projection below their cusps (Sasaki et al., 2003: figs. 12, 14).

Major differences in radular characters exist mainly in the central and lateral teeth among Neritopsina. In contrast to most neritopsines, including *Shinkailepas*, the central tooth is absent in the Neritiliidae (Kano & Kase, 2002, 2003, in press; Kano et al., 2003), *Neritopsis* (Warén & Bouchet, 1993: fig. 3D), and *Titiscania* (Bergh, 1890; Taki, 1955). The lateral teeth morphology is considerably variable among neritopsines and it is difficult to generalize. For example, in the Neritidae, the first laterals are transversely elongate, and the fourth laterals are thickened in shield-like form. The Neritiliidae (Kano & Kase, 2002, 2003, in press; Kano et al., 2003) and most helicinoideans (e.g., Thompson, 1980; Sasaki, 1998; Richling, 2004) have obliquely elongate outermost lateral teeth with sharp serrations, and lateral teeth are more reduced in *Neritopsis*, *Titiscania*, and the Hydrocenidae (Ponder, 1998: fig. 15.76). The presence of prominence below cusps in the marginal teeth (Kano & Kase, 2002: fig. 8) is known in the Neritiliidae, *Neritopsis*, and *Titiscania* (Kano & Kase, 2000, 2002), but not in others.

The configuration of the radular sac has not hitherto been focused in the studies of the Neritopsina. Recently, Kano & Kase (2002) pointed out that in the Neritopsina the length of radular sac can be categorized into two groups. A long, looped radular sac is typical of the Neritiliidae, *Neritopsis* and *Titiscania*; by contrast, a short straight type occurs in the Neritidae, Phenacolepadidae, and Helicinidae (Kano & Kase, 2002). *Shinkailepas myojinensis* (Fig. 5), *S. kaikatensis* (Okutani et al., 1989: fig. 15), and *Olgasolaris tollmanni* (Beck, 1992: fig. 3B) have the latter type.

The esophagus of the Neritopsina exhibits similar structure throughout the group (Sasaki, 1998): (1) It consists of the anterior and posterior esophagi only, lacking the differentiation of a mid-esophagus, (2) the anterior esophagus is sectioned into a centrally situated, dorsal food channel and lateral esophageal pouches with the anterior esophageal glands inside, and (3) the posterior part of the lateral esophageal pouches are separated as the posterior esophageal glands. The esophagus of *S. myojinensis* matches this generalization well.

A peculiar shaped esophagus was recently described in the Neritiliidae by Kano & Kase (2002). The anterior esophageal glands are extremely elongated posteriorly as separated pouches and overlie the posterior esophageal glands. This double structure of esophageal glands is not known in other neritopsines including *Shinkailepas*.

The posterior esophageal glands in *S. myojinensis* are complicatedly infolded and tightly enclose the radular sac with a narrow interstitial space (Fig. 9F). This morphology apparently differs from that of other neritopsines, including the Neritiliidae (Kano & Kase, 2002: fig. 5D). Hence, the structure of this part may be of sufficient systematic value, but cross-sectional morphology of the glands have not been described for comparison in the rest of neritopsines.

Another distinctive character of the Neritiliidae is the presence of the floor glands arising from anterior esophageal floor (Kano & Kase, 2002). The glands are paired blind sacs that open from the posterior side of the floor of the anterior esophagus and consist of two glandular cells ciliated differently and stained differentially with haematoxylin (Kano & Kase, 2002: fig. 3C). The identical glands were not found in sections of equivalent position in *S. myojinensis*.

The stomach of the Neritopsina consists of a cuticularized area, gastric shield with a short reflected tooth, paired (major and minor) typholosoles on the ventral side, a ciliated intestinal groove between the typhlosoles, and a short gastric caecum (Fretter, 1965; Sasaki, 1998; Kano & Kase, 2002). Differences in the stomach structure among the Neritopsina is not very conspicuous. The Neritiliidae have only a single connection between stomach and digestive glands (Kano & Kase, 2002), whereas two or more openings of digestive glands occur near sorting area in the stomach of other neritopsines (e.g., Bourne, 1909, 1911; Fretter, 1965, 1984; Sasaki 1998). It is uncertain at present whether the number of the openings is dependent on body size or phylogentetically fixed.

Excretory System: Neritopsine excretory system is composed of the auricle with podocytes as an ultrafiltration site, renopericardial duct as a conduit of primary urine, and a single left kidney for osmoregulation and excretion (Estabrooks et al., 1999). Within the Neritopsina, two types of kidneys are known to date: (1) In the Neritidae, Phenacolepadidae, and Helicinidae, the kidney is composed of glandular region, non-glandular bladder, and short ureter (Little, 1972; Sasaki, 1998; Estabrooks et al., 1999). (2) In the Neritiliidae, the wall of kidney is simple, not specialized into glandular and non-glandular areas (Kano & Kase, 2002). The kidney of *S. myojinensis* belongs to the latter type. Functional differences of these two types are not clear, though development of infoldings in the glandular area of the former type is obviously related to functional advantage to increase its surface area.

Circulatory System: In the heart of gastropods the ventricle is always single, but it is attached by paired or unpaired auricle(s), depending on taxa. In *S. myojinensis*, the pericardium contains two (right and left) auricles and a single median ventricle. The right auricle is obviously present in *S. myojinensis* but greatly reduced. A vestigial auricle is also present in *Cinnalepeta* (Sasaki, 1998) and *Phenacolepas* (Fretter, 1984). In other neritopsines, the right auricle is present in the Titiscanidae and Cerisidae of the Helicinidae but absent in the Hydrocenidae, Proserpininae, and Helcinidae (Sasaki, 1998). The ventricle is penetrated by the rectum in the Neritopsina, except the Hydrocenidae and Helicinidae (Sasaki, 1998).

Although details have not been studied hematologically, the presence of erythrocytes is a possible general feature of phenacolepadids. They are discoidal and biconcave in *Phenacolepas* (Fretter, 1984) and *Cinnalepeta* (Sasaki, 1988: fig. 85d). The animals of these two genera are red in fresh live condition, but immediatedly turned pale after the death by fixation. In *Shinkailepas* aff. *kaikatensis* from the Mariana Back-arc Basin, the red color is also very vivid only while living (Hasegawa et al., 1997). Hence, species of *Shinkailepas* are presumed to have erythrocytes. The form of haemocytes in *S. myojinensis*, however, do not seem discoidal but spherical (Fig. 10B).

Female Reproductive System: The female organs of neritopsines consist mainly of the ovary, oviduct, pallial oviduct with albumen and capsule glands, and vaginal duct with two saclike appendages.

It is well known that the number of reproductive opening(s) is different in female among neritopsine taxa. In *S. myojinensis*, pallial oviduct and vaginal duct have their own openings (diaulic). In contrast, female reproductive system is triaulic with an additional enigmatic duct in *Septaria* (Sasaki, 1998) and monaulic in *Titiscania* (Marcus & Marcus, 1967) (neritiliids do not have a monaulic system as previously believed (Kano & Kase, 2002). A diaulic reproductive system is most common among Neritopsina.

Separation of the vaginal duct from the pallial oviduct is a common feature in most neritopsines, and it is also true of *S. myojinensis*. Characteristically, the vaginal duct in *S. myojinensis* is associated with three structures: (1) a transverse slit of the vaginal opening below the anterior part of pallial oviduct, (2) the receptaculum seminis near the vaginal opening, and (3) the "posterior sac" below the posterior part of the pallial oviduct.

A slit-like vaginal opening in the anterior position is also described in *Olgasolaris* (Beck, 1992). In the Neritiliidae, the vaginal opening is also a slit but located posteriorly (Kano & Kase, 2002). It is a small pore, not a long slit, in *Phenacolepas* (Fretter, 1984), *Cinnalepeta*, the Neritidae, and Helicinidae (Sasaki, 1998).

An anteriorly situated receptaculum seminis near the vaginal opening in *S. myojinensis* is unique among the Neritopsina. In other groups, receptaculum seminis has been identified in various positions (e.g., Sasaki, 1998), but it has not always been verified on histological basis. The presence of oriented spermatozoa in its epithelium (Fig. 15A) is the most reliable criterion for this identification.

The "posterior sac" of the vaginal duct may also be peculiar to *S. myojinensis*. Its inner wall is heavily folded characteristically. Because no sperm or egg was contained in sectioned specimens, its actual function in reproduction could not be detected. An equivalent structure is unknown in *Olgasolaris* (Beck, 1992) and *Phenacolepas* (Fretter, 1984), or lacking in *Cinnalepeta* (Sasaki, 1998: fig. 84). The spermatophore sac in the Neritidae and *Cinnalepeta* (Sasaki, 1998: figs. 76, 84) cannot be homologized due to the differences in topological relationships with other reproductive organs.

It is uncertain whether *S. myojinensis* produces spermatophores or not. The spermatophores are generally known to occur in neritopsine gastropods (Robertson, 1989, reviewed gastropod spermatophores). In the Neritidae, intact spermatophores are often contained in the spermatophore sac in female (Sasaki, 1998: figs. 76c–d), and the formation of the spermatophore sheath is also observable in the seminal vesicle of the male. In this case, the formation of spermatozoa is undoubted. But in *S. myojinensis*, no spermatophore was found in any section of female and male reproductive systems.

The pallial oviduct of *S. myojinensis* is enclosed by two kinds of glands that correspond to the albumen and capsule glands, as is generally found in gastropods that produce egg capsules. The albumen gland is further divisible into two parts in *S. myojienesis*. The similar division is also known in the Neritiliidae, Neritidae, and shallow-water phenacolepadids (Sasaki, 1998; Kano & Kase, 2002), but not in non-neritopsine gastropods.

Some neritopsines are known to have a mineral-containing "crystal sac" and cover egg capsule with minerals from the sac. The absence of the crystal sac was verified in *S. moyojinensis* in this study and in the Neritiliidae by Kano & Kase (2002). Meanwhile, the sac is distended with calcified grains in the Neritidae (Sasaki, 1998: fig. 77h). Marcus & Marcus (1967) reported the crystal sac in *Titiscania*, but it is questionable (Kano & Kase, 2002). Probably the possession of the crystal sac is restricted to the family Neritidae.

Internally fertilizing gastropods may develop a particular structure conveying eggs from the female opening to the foot through the neck region. The Neritiliidae have the neck furrow and female flap on the right side in the female (Kano & Kase, 2002: figs. 2B, 15B), and presumably eggs are conveyed along a ciliated furrow in oviposition. The female flap in Neritiliidae is possibly homologous to the structure identified as the ovipositor in *Phenacolepas* by Fretter (1984) (Kano & Kase, 2002). In *S. myojinensis*, a corresponding structure was not found in the right pedal region. Because actual behavior of egg deposition has never been observed in phenacolepadids, functional significance of right neck-foot morphology is unclear.

Male Reproductive System: Male reproductive organs of neritopsines generally comprise the testis, vas deference, seminal vesicle, pallial male gonoduct with prostate, and penis. All of these organs represent a common element of the male reproductive system possessed universally by internally fertilizing gastropods.

The seminal vesicle is formed in convoluted part of vas deference in some Neritopsina, for example, Neritidae including *Bathynerita* (Warén & Bouchet, 1993), shallow-water phenacolepadids (Sasaki, 1998), and *Shinkailepas*. By contrast, in the Neritiliidae, the seminal vesicle is double and different from tightly convoluted type (Kano & Kase, 2002). In the Helicinidae, it is simple, not entangled (Thompson, 1980; Sasaki, 1998). Thus, the configuration of vas deference is a useful character defining some higher taxa in Neritopsina.

It is common pattern in Neritopsina that the male pallial gonoduct is covered with the annex gland posteriorly and the prostate anteriorly. The formation of the prostate pouch on the dorsal side in *Shinkailepas* is a distinctive character not known in other neritoideans.

The position and structure of copulatory organ in male is greatly variable across various groups of gastropods. In Neritopsina, the penis arises unexceptionally from inner side of the right cephalic tentacle, if present. The seminal groove in the penis extends along right lateral margin in *S. myojienesis* (Fig. 14A) but on dorsal surface in *Olgasolaris tollmanni* (Beck, 1992: pl. 5, fig. 6).

The penis in male arises in a position equivalent to the right cephalic lappet of female. This may suggest that the penis has arisen as a modified cephalic lappet. The development of the penis is, however, independent of that of the cephalic lappets, because neritids and *Cinnalepeta* lacking cephalic lappets have the penis in a similar position (Sasaki, 1998). In the Neritiliidae, which entirely lack the cephalic lappets, the penis is rudimentary in *Pisulina* or absent in *Neritilia* (Kano & Kase, 2002).

A ciliated papilla on the ventral side of the penis (Figs. 14A–B) is unique to *S. myojinensis* among Neritopsina. But, the presence or absence of equivalent structure in other neritopsines is actually uncertain, because the penis has not been observed from its ventral side in the previous studies. Its function remains entirely unidentified.

Nervous System: The nervous system of *S. myojinensis* consists of a hypoathroid circumesophageal nerve ring, non-streptoneurous visceral nerve with characteristic configuration, a pair of thick pedal cords, and other thin peripheral nerves.

The circumesophageal nerve ring of *S. myojinensis* is rather concentrated for that of neritopsines, compared to other anatomically examined species (Fretter, 1984; Sasaki, 1998; Kano & Kase, 2002). Especially, pleural and pedal ganglia are closely situated and almost fused with each other. The positions of cerebral and buccal ganglia are similar to those of various rhipidoglossate gastropods. Pleural ganglia have their own commissure, which is a general character peculiar to neritopsine gastropods.

The presence of labial commissure below sublingual pouch is also a common feature throughout the Neritopsina. A similar commissure also exists in the Patellogastropoda in general, but it is different from that of neritopsines in that the labial ganglia are developed on the commissure. The labial commissure without ganglia also occurs in the Ampullariidae (Berthold, 1991), which shows a comparable state in a different clade of gastropods.

It is interesting that the visceral part of nervous system does not form a complete loop in some neritopsines. Such a condition is also known in *Phenacolepas* (Fretter, 1984), neritiliids (Kano & Kase, 2002), and *S. myojinensis*. In the Neritidae, it is complete, and the supraesophageal loop can be traced over the anterior esophagus from the right pleural ganglion (e.g., Sasaki, 1998: fig. 79d). The incomplete visceral loop is possibly secondary reduction rather than primary condition, because remaining gastropods and other molluscs generally have a complete visceral/ lateral nerve loop.

Sense Organs: The eyes are often reduced or secondarily lost in various organisms living in such dark environments as caves and the deep sea. *Shinkailepas myojinensis* is distinct from other neritopsines in that the eyes are certainly present but markedly vestigial. They are represented only by pigmented cells, lacking lens, and deeply embedded below epithelium of the eye stalks. In contrast, the eyes of shallow-water and terrestrial neritopsines are filled with the lens and covered with the cornea. Another exception to this generalization is the Neritiliidae which have open eyes without lens and cornea (Kano & Kase, 2002). They are considered to have been modified due to adaptation to cryptic habitat. The eyes in *Shinkailepas* are probably non-functional and reduced in the dark deep-sea environment.

There seems to be some differences in the structure of osphradium among Neritopsina. In aquatic neritopsines, the osphradium is located along the left shell muscle, and defined by central zone, paired lateral zones, and pigment bodies at ultrastructural level (Haszprunar, 1985). However, it is two-folded with a longitudinal central groove and devoid of clearly ciliated lateral zones in *S. myojinensis*. A similar longitudinal groove on the central zone is also present in *Bathynerita* (Warén & Bouchet, 1993), but obviously absent in other neritopsines, such as *Nerita* (Haszprunar, 1985; Sasaki, 1998: fig. 77d).

The position of the statocysts is somewhat variable among neritopsines. They are located on the posterodorsal side of the pedal ganglia in *S. myojinensis,* and also the Neritidae (Sasaki, 1998) and Helicinidae (Bourne, 1911). In the Neritiliidae, their position is shifted more anteriorly (Kano & Kase, 2002).

Each statocyst contains either single statolith or many statoconia, depending on taxa in gastropods (Ponder & Lindberg, 1997). Even within Neritopsina, there are both of these two types. At least two examples are known: statocysts in the Neritiliidae (Kano & Kase, 2002) and statoconia in *S. myojienesis*. Their condition in other taxa have not been clearly described based on histological observations. The systematic and functional significance of statocyst contents is still unclear throughout neritopsines.

Systematic Implications

The allocation of *Shinkailepas* to Neritopsina was corroborated by sufficient numbers of anatomical characters. The features shared with other neritopsines in general (Sasaki, 1998: 220–221) are: (1) a multispiral globular protoconch with growth lines in aquatic members, (2) a single left ctenidium lacking skeletal rods and bursicles, (3) a single osphradium along the left shell muscle, (4) three (anterior, posterior, and median) elements of odontophoral cartilages, (5) the dorsal levator muscles of odontophore, (6) the tensor muscles of anterior cartilages, (7) the absence of the salivary gland, (8) the esophageal glands separated from the esophagus posteriorly, (9) a small crescent-shaped gastric caecum, (10) the labial commissure without labial ganglia, (11) one-side origin of visceral loop from right side, and (12) the pleural commissure. Some more characters were previously regarded as general neritopsine features (Sasaki, 1998), but at least two, eye and kidney structure, were rejected as revealed in recent studies. As discussed above, closed eyes with vitreous body is not found in Neritiliidae and *Shinkailepas*. The kidney in neritopsines is not always clearly differentiated into glandular and non-glandular sections.

Within Neritopsina, anatomical comparison suggests that *Shinkailepas* is included in the superfamily Neritoidea, which currently includes the Neritidae and Phenacolepadidae. The Neritoidea is mainly diagnosed by characters of digestive and reproductive organs, such as (1) a well-developed oral lappet, (2) the sublingual glands, (3) the median levator muscles of odontophore, (4) the radular formula n-4-1-4-n, (5) two auricles with right one smaller, (6) the capsule and albumen glands in female, (7) the annex gland in male gonoduct, and (8) the penis from the inner side of right cephalic tentacle. This definition of the superfamily with above characters is revised from that of Sasaki (1998).

Concerning the relationships with other neritopsine families, *Shinkailepas* shares no anatomical characters uniquely with three helicinoidean families (Bourne, 1911; Thomson, 1980; Sasaki, 1998) or Neritiliidae (Kano & Kase, 2002). The remaining families, the Hydrocenidae, and the Neritopsidae (including Titiscanidae: Kano et al., 2002), have not been described sufficiently for comparison. In molecular characters, Kano et al. (2002) revealed the relationships (Neritopsidae (Hydrocenidae (Helicinidae + Neritiliidae) (Neritidae + Phenacolepadidae))) based on 28S rRNA sequences. Therefore, it is highly likely that neritoidean groups including *Shinkailepas* are phylogenetically distinct from non-neritoidean families within the Neritopsina.

The Neritoidea is currently divided into the Neritidae and Phenacolepadidae, and *Shinkailepas* is assigned to the latter (Beck, 1992; Warén & Bouchet, 2001). Phenacolepadids, including shallow-water and vent/seep-endemic groups, share a rather limited number of unique characters compared to other neritopsine families. Their common characters are: (1) transversely elongated first lateral teeth of the radula, (2) longitudinally tall fourth lateral teeth, and possibly (3) erythrocytes. The absence of hypobranchial gland may be another general character of the family, but its state is not certain in *Olgasolaris*. There are some more similarities, but in fact, they are not specific to phenacolepadids. For example, the cephalic lappets are also described in neritid *Bathynerita* (Warén & Bouchet, 1993), a cephalic penis also occurs in the Neritidae, two shell muscles without division are found in *Septaria* (Sasaki, 1998).

Within phenacolepadids, two major groups, deep-sea and shallow-water ones, can be clearly diagnosed. Two deep-sea vent/seep-associated genera, *Shinkailepas* and *Olgasolaris*, have similar characters in common (Table 2): (1) shell canals and pores penetrated by the mantle processes, (2) a trapezoidal, non-spiral, calcified operculum, (3) the cephalic lappets, (4) the epipodial fold, (5) the absence of circumpallial tentacles, (6) the intestine with two loops only, and (7) an anteriorly positioned, slit-like vaginal opening. Most of these similarities are distinctive of these two genera, suggesting their close phylogenetic relation.

In contrast to two deep-sea genera, shallow-water phenacolepadids (*Phenacolepas* + *Cinnalepeta*) are united by (1) the absence of shell pores and mantle processes, (2) a weakly developed, spiral operculum with apophysis, if present, (3) the absence of cephalic lappets, (4) the absence of epipodial folds, (5) the circum-pallial tentacles, (6) complex loops of intestine, and (7) a small pore-like vaginal opening.

At the species level, there are some anatomical differences among four described species of *Shinkailepas*. The comparison with *S. myojinensis* revealed that in *S. briandi* Warén & Bouchet, 2001, (1) the eye stalks ("eye-lobes") are very weakly developed, (2) the epipodial fold in neck region is prominent on the left and right sides, (3) the penis is more elongated, and (4) the posterior margin of the epipodial fold is not divided into triangular tentacles. Likewise, in *S. kaikatensis* Okutani, Saito & Hashimoto, 1989, (1) the eye stalks are not developed, (2) the penis is more acutely pointed, and (3) the number of tentacles on the epipodial folds ("pedal papilla") is smaller (11 in *S. kaikatensis*, 11–19 in *S. myojinensis*). In *S. tufari* Beck, 1992, the number of tentacles on epipodial folds is largest (20–22) among known species, but other characters have not been described in detail. Thus, eye stalks, epipodial folds in neck and posterior pedal regions, and penis are useful species-level taxonomic characters in the external features of the soft part. For shell, radular, and opercular characters at species level, see Sasaki et al. (2003).

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APPENDIX: Abbreviations used in descriptions

a = anus
aca = anterior cartilage of odontophore
acv = afferent ctenidial vein
ag = albumen gland
ag I = albumen gland I
ag II = albumen gland II
al = anterior levator muscle of odontophore
ang = annex gland
apd = anterior pedal gland
apg = anterior pedal groove
apl = anterior pallial gland
at = anterior tensor muscle of odontophore
bcv = buccal cavity
bg = buccal ganglion
c = ctenidium
cc = cerebral commissure
cdc = cerebropedal connective
cg = cerebral ganglion
clp = cephalic lappet

cp = cuticularized plate
cpc = cerebropleural connective
cpg = capsule gland
ct = cephalic tentacle
dbt = dorsal buccal tensor muscle
df = dorsal fold of esophagus
dfc = dorsal food channel of anterior esophagus
dg = digestive gland
dgo = opening of digestive gland to stomach
dl = dorsal levator muscle of odontophore
dps = duct of posterior sac
e = eye
ecv = efferent ctenidial vein
ef = epipodial fold
es = eye stalk
ev = esophageal valve
f = foot
fo = female opening of gonoduct
gc = gastric caecum
gst = tooth of gastric shield
i = intestine
if = inner fold of mantle margin
ivp = inner ventral protractor muscle of odontophore
k = kidney
ko = kidney opening
la = left auricle
lca = labial cartilage
lep = lateral pouch of anterior esophagus
ln = labial nerve
lp = lateral protractor muscle of odontophore
lpr = lateral protractor muscle of subradular membrane
lsm = left shell muscle
m = mouth
mca = median cartilage of odontophore
ml = median levator muscle of odontophore
mm = mantle margin
mo = male opening of gonoduct
mp = mantle process
mpg = male pallial gonoduct
mpr = median protractor muscle of subradular membrane
mt = mantle
oap = outer approximator muscle of cartilages
of = outer fold of mantle margin
ol = oral lappet
os = osphradium
ot = oral tube
ovd = oviduct
ovp = outer ventral protractor muscle of odontophore
p = penis
pc = pericardium
pca = posterior cartilage of odontophore
pcd = pedal cord
pcv = pallial cavity
pd = posterior depressor muscle of odontophore
pds = pedal sole
pdt = postdorsal buccal tensor muscle
pe = posterior esophagus
pg = periostracal groove
plc = pleural commissure
plg = pleural ganglion
pls = pallial sinus
pn = pallial nerve
po = pallial oviduct
pr = prostate
prp = prostate pouch
ps = posterior sac of vaginal duct
ptg = post-tentacular gland
ra = right auricle
rds = radular sac
rdt = radular teeth
rev = retractor muscle of esophageal valve
rrs = retractor muscle of radular sac
rs = seminal receptacle
rsm = right shell muscle
rsr = retractor muscle of subradular membrane
sbv = subesophageal part of visceral loop
sc = statoconia
slg = sublingual gland
slp = sublingual pouch
sn = snout
srm = subradular membrane
st = stomach
sta = statocyst
sv = seminal vesicle
t = testis
tac = tensor muscle of anterior cartilage
tbf = transverse buccal fold
tn = tentacular nerve
v = ventricle
vad = vaginal duct
vao = vaginal opening
vap = ventral approximator muscle of cartilages